public library. While I do not solicit or particularly enjoy speaking engagements, I fill them occasionally. . . . It is so fine and warm today that I think I will go fossil hunting this afternoon." For a man retired and eighty years old he certainly was enjoying life to the fullest, doing exactly what he wanted to do — and he seemed so well equipped to do it!

During his life time Ernest Palmer joined many scientific organizations, among them: the American Fern Society, the American Association for the Advancement of Science, the American Society of Plant Taxonomists, the Boston Mineral Club, the Botanical Society of America, the Missouri Archaeological Society, the New England Botanical Club (past president 1944-1945), and the St. Louis Academy of Science.

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SOME OBSERVATIONS ON FLOWERING IN RUELLIA (ACANTHACEAE)

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During the past four years the authors have been making systematic observations on transplants and natural populations in *Ruellia*, commonly referred to as "wild petunia".[2] Although primarily tropical and subtropical in distribution, this genus is represented in eastern United States by 11 species of low, perennial herbs with opposite leaves and large blue or lavender, funnelform flowers.

Ruellia is a difficult genus for the taxonomist because of the absence of reliable characters in certain species. Twenty varieties and forms have been described in *R. caroliniensis*

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[2]We wish to thank the following persons for their courtesy in supplying us with *Ruellia* materials for greenhouse cultures: Drs. J. T. Baldwin, R. E. Woodson, R. K. Godfrey, W. H. Duncan, J. D. Ray, G. S. Winterringer, Mr. K. E. Bartel and Mrs. T. C. Lacey. Voucher specimens for these cultures are deposited in the Herbarium of the University of South Florida.

(Walt.) Steud. and *R. humilis* Nutt. (Fernald, 1945; Tharp and Barkley, 1949) largely on the basis of minor character differences. Fernald did much to clarify the nomenclature, but his classification of eastern species is complex and difficult to use. It is now apparent that a major cause of this is a poor understanding of the reproductive biology of these plants. Monographic treatments of *Ruellia* have been based almost entirely on herbarium specimens, and no attempt made to investigate plants in culture or extensively in the field.

This report attempts to clarify the relationship of cleistogamy to normal flower-production (chasmogamy) and to describe the reproductive behavior of certain eastern U. S. species as far as they have been investigated. Four species are included in this discussion, all except one having been observed in both garden and greenhouse cultures, and in the field. In these species the following kinds of breeding systems have been observed: obligate and facultative cleistogamy, the latter condition either coincident with chasmogamy or sequential; obligate and facultative chasmogamy; chasmogamy involving normal-sized corollas, and these either long-styled, medium-styled, or short-styled; chasmogamy involving small-sized corollas, called here "miniatures", that are approximately half as long as normal flowers; facultative proterogyny was regularly observed in some greenhouse plants, although synanthesis is usual in *Ruellia;* finally, polygamy was noted in two species discussed in this paper, involving apetalous, pistillate flowers in one and staminate, petaliferous flowers in the other.

Ruellia strepens L. (5 natural populations examined, Ohio and Virginia; 3 greenhouse cultures, Ohio and Virginia). This species has been studied the most extensively of all and is perhaps the best known one to taxonomists because of its wide distribution in the Middle West. It is readily separable from other eastern species by means of its lanceolate calyx lobes; other species have linear or setiform sepals. *Ruellia strepens* is remarkably uniform between and within populations. Chasmogamous flowering begins in late April and continues to mid-July, followed by small, greenish-

yellow cleistogamous flowers produced from late June to the first frost and borne in sparse to congested subsessile, axillary glomerules. Plants occasionally do not produce any flowers for a period between reproductive phases.

Ever since Gray (1878) formalized a varietal status for cleistogamous plants of *R. strepens*, differences of opinion have existed as to the nature of such plants. Chapman (1884) reported late flowers sometimes set fruit in the bud. McCoy (1937), after observing a single garden transplant, reported cleistogamy sequential to chasmogamy in the same individual. Nevertheless, recent monographers (Fernald, *ibid.*; Tharp and Barkeley, *ibid.*) have continued to describe cleistogamous specimens as either forma *cleistantha* (Gray) S. McCoy or var. *cleistantha* Gray. We have observed hundreds of plants of *R. strepens* in a total of 5 populations. In all instances cleistogamy regularly follows chasmogamy except that young plants appear to be exclusively cleistogamous in their first year of flowering. In addition, greenhouse cultures of plants collected during the chasmogamous phase later produced cleistogamous flowers. Immediate environmental factors strongly influence the production of flower-types. Thus, cleistogamy is precocious in sear, open habitats, whereas chasmogamous flowering is prolonged by shade, moisture, and rich soil. Moreover, cleistogamous plants may revert to chasmogamy as a result of prolonged cool or cloudy weather. Also, chasmogamy may coincide with cleistogamy for a period of time. Greenhouse cultures of this species have never flowered chasmogamously, even in May and June, but produce only closed flowers; garden transplants produce both chasmogamous and cleistogamous flowers.

The earliest flowers of *R. strepens* apparently are seldom pollinated and thus rarely form seeds. Observations of natural populations reveal that, although abundantly produced, chasmogamous flowers are infrequently visited by insects. Early seed-production is mostly destroyed by Lepidopterous larvae, but insect-depredations taper off in early autumn. Plants thus appear to produce seed abundantly in their autumnal cleistogamous phase. Although

Fernald noted the low seed-production of chasmogamous flowers, and the correspondingly high production of cleistogamous ones, he failed to explain why his open-flowered variety appeared to be more common than the closed-flowered variety.

Three kinds of chasmogamous flower-structures have been observed in this species: (1) early chasmogenes with anthers about the throat orifice and with the stigma much exserted on a long style; (2) a later-appearing chasmogene, but one which may appear coincidentally among earlier flowers, with anthers and stigma borne at approximately the same level; (3) a less common type, with a short style resulting in the stigma being below the level of anthers. Thus, partial heterostyly exists in *R. strepens* which, even in chasmogamous flowers, tends to favor inbreeding. Open-flowers last only part of the day; ordinarily anthesis occurs soon after sunrise and corollas fall from the receptacle shortly after noon. *Ruellia strepens* apparently is a habitually inbreeding species with very few biotypes, these hardly dissimilar morphologically, resulting in homogeneous populations.

Ruellia caroliniensis (Walt.) Steud. (10 natural populations examined, Florida, North Carolina, South Carolina, Virginia; 11 greenhouse cultures, Virginia, Kentucky, Florida, Georgia, North Carolina, South Carolina). This species has been described as the most perplexing *Ruellia* of eastern North America (Fernald, *ibid.*). Field work has been carried out in Virginia, North and South Carolina, and Florida. In this region a number of varieties and forms have been described by Fernald, none of which is accepted by Gleason (1952). Judging from the variations in greenhouse and garden transplants, *R. caroliniensis* is apparently the most racially complex member of the genus in North America. Few, if any, of these races may deserve taxonomic recognition, but definite taxonomic evaluations can not be made at this time. Although the species varies widely, plant-to-plant variability within populations is negligible. The interpopulation variability of *R. caroliniensis* probably is correlated with the wide range of habitats in which this species can be found.

Both chasmogamous and cleistogamous flowers are produced in a manner essentially similar to *R. strepens*. Chasmogamous flowers are produced abundantly in the spring but apparently rarely set fruits. Cleistogamous flowers, previously unreported for this species, occur in the summer and early autumn with abundant seeds produced. In *R. caroliniensis* races have been grown in the greenhouse that form only chasmogamous flowers, but if hand-pollinated, produce normal fruits with seeds that germinate readily. Short-styled and long-styled flowers occur in the same individual with long-styled flowers predominant. One greenhouse race was quite variable, producing staminate flowers, "miniature" flowers, and exhibiting proterogyny occasionally. Another race produced only cleistogamous flowers.

Ruellia humilis Nutt. (2 natural populations examined, Ohio and Virginia; 10 greenhouse cultures, Illinois, Texas, Kansas, and Ohio). This species, occurring primarily in the prairies and plains of central United States, has been segregated into a number of varieties. Fernald reports cleistogamy as rare, but observations show the reverse to be true. Flowering may be chasmogamous or cleistogamous, sequentially or coincidentally. Cleistogamous flowers are produced more abundantly in all races as the season progresses. Chasmogamous flowers with the long-exserted stigmas predominate, but one greenhouse culture occasionally produced short-styled ones. This same race regularly formed chasmogenes and cleistogenes simultaneously rather than sequentially as is generally true for the species. In *R. humilis* greenhouse observations revealed that, although pollinators were absent, chasmogamous flowers usually formed fruits. This was owing to the manner in which the corolla was shed from the receptacle, resulting in the epipetalous stamens coming in contact with the exserted stigma. This same mechanism was observed in other species but not so regularly as in *R. humilis*.

Ruellia pedunculata Torr. (6 greenhouse cultures, Texas) This is a remarkably stable species, morphologically, that characteristically produces long-stalked blue, lavender or white flowers. It is distributed widely in Texas, the Ozark-

ian uplands and into southern Illinois. The reproductive systems of this species, as reflected by the kinds of flowers produced, are among the most complex of any investigated this far.

Cleistogamy occurs regularly in all greenhouse cultures along with open-flowers, although apparently this has not been noted before. The closed-flowers measure about 1.0 cm. long, are white with greenish-brown tips, and may occur coincidentally with open flowers or sequentially with open flowers. Evidentally, here, as in *R. humilis* and *R. caroliniensis* there exist at least two races differing in the timing of flower-production. Partial heterostyly, similar to that in *R. strepens*, occurred frequently in one race. Long-styles measure 2.5-3.0 cm. long and short-styles only 1.0-1.5 cm. long, well within the throat of the corolla and below the stamens. Long-styled flowers failed to form fruits when protected from insects and not hand-pollinated. Short-styled flowers always formed fruits.

A fourth kind of flower appeared in two cultures. This was an apetalous, pistillate flower with a short-style. That this was not merely a cleistogamous flower that had shed the corolla was established by repeated observations. The occurrence of these unisexual flowers was sporadic but coincident with open-flowers. All classes of flowers were functional and could form normal fruits, but apparently in nature the species is habitually self-pollinated.

No field work has been possible with *R. pedunculata* as yet, but observations reported here are based on 80 greenhouse transplants distributed in 11 different races. There is relatively little morphological variation within and between these races despite the fact that most of the collections came from regions of sympatry with *R. caroliniensis* and *R. humilis*. *Ruella pedunculata* can be hybridized with these two species but natural hybrids are unknown at the present time.

CONCLUSIONS

Breeding experiments with greenhouse and garden cultures are in early stages and only preliminary results have been obtained (Long, unpubl.), but apparently all classes

of flowers in these four species are functional and can form fruits with viable seeds. Field observations, however, indicate that *Ruellia* species are habitually self-pollinated. The relatively small amount of morphological variation in *R. strepens* and *R. pedunculata* suggests that outcrossing seldom takes place. On the other hand, Long (1961) adduced evidence from herbarium samples and hybridization experiments that crossing of *R. humilis* and *R. caroliniensis* probably does occur and that at least some of the apparent intergraduation between these species may be attributed to natural hybridization. More detailed and extensive observations are needed on species thus far only partially investigated, such as *R. ciliosa*, *R. heteromorpha* and *R. purshiana* as well as on numerous North American species as yet poorly known. Apparently, however, *R. strepens*, *R. caroliniensis*, *R. humilis*, and *R. pedunculata* are examples of plants that are functionally autogamous but with many of the typical flower structures of allogamous ones.—DEPARTMENT OF BOTANY AND BACTERIOLOGY, OHIO WESLEYAN UNIVERSITY, DELAWARE, OHIO; AND ROUTE 3, MADISON HEIGHTS, VIRGINIA.

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